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云南禄丰、元谋晚中新世古猿地点始鼠科化石[1)]

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始鼠科(Eomyidae)是一类绝灭了的啮齿类动物,渐新世和中新世时广布全北区,但亚洲远没有欧洲和北美常见。中国含始鼠类化石地点不多,发现的属只有渐新世的 *Eomys*、*Eomyodon* 和 *Pseudotheridomys*,以及中新世的 *Keramidomys* 和 *Leptodontomys* (Zheng and Li, 1982; Falhbusch et al., 1983; Wang and Emry, 1991; Qiu, 1996; Wang, 2002)。

本文描述的云南始鼠类化石,系1983年在禄丰石灰坝和1999、2000年在元谋雷老两个古猿地点采集到的。材料不多,但至少代表始鼠科的两个新属,为我国惟一采自南方,并与古猿类共生的稀少啮齿类动物。新种的模式产地均为禄丰石灰坝。

石灰坝和雷老小哺乳动物化石的研究表明,这两个"地方动物群"的时代均属中国陆相哺乳动物分期中的晚中新世保德期,与欧洲陆相哺乳动物 MN11 带上部或 MN12 带下部相当(Qiu and Storch, 1990; Qiu and Qiu, 1995; Qiu, 1995)。竹鼠类(rhizomyids)、仓鼠类(cricetids)和鼠类(murids)的演化水平,似乎指示了元谋动物群的时代略早;根据与西瓦立克竹鼠生物地层学和磁性地层学的对比,估计石灰坝动物群距今至少有 8 Ma,而雷老可能达 9 Ma (Flynn et al., 1998; Ni and Qiu, 2002; Storch and Ni, 2002)。

近始鼠属(新属) *Plesieomys* gen. nov.

奇特近始鼠(新属新种) *Plesieomys mirabilis* gen. et sp. nov.

属的特征 丘齿型始鼠类中个体较小的一属。颊齿舌侧和唇侧主尖近同等发育,横向齿脊发育弱。M1~2 舌侧前边脊几乎缺失;中脊长度中等,末端往往肿胀成小尖;后脊发育弱;舌侧谷大体对称。m1~2 的下次脊常常中断或缺失,前边脊和后边脊短而弱,第一及第四下内谷狭窄。

种的特征 同属的特征。

新属与 *Eomys* 有相似的形态特征,可能为其后裔。它以牙齿横脊发育弱、上臼齿中脊末端肿胀而区别于其他丘齿型始鼠。该属和北美的 *Pseudadjidaumo* Lindsay 属有点相似,但具体的系统关系还不清楚。

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异始鼠属(新属) *Heteroeomys* gen. nov.

云南异始鼠(新属新种) *Heteroeomys yunnanensis* gen. et sp. nov.

属的特征 丘齿型始鼠。颊齿舌侧和唇侧的主尖多少有点不同等发育,具有中等长度的中脊。上臼齿舌侧前边脊缺失,但前边脊长、伸达舌侧,并直接与原尖连接;上臼齿的后脊、下臼齿的前边脊和下次脊发育弱,甚至中断。

种的特征 同属的特征。

新种与 *Plesieomys mirabilis* 同为丘齿型始鼠,但牙齿尺寸比后者的略大,齿冠稍高,内、外侧主尖不同等发育。其上臼齿前边脊伸达舌侧并直接与原尖连接的这一形态特征,不仅未见于奇异近始鼠,而且也未发现于迄今所知的丘齿型始鼠。

与 *Eomys* 比较,新属的牙齿形态既保留了这一原始丘齿型始鼠的特征(如相对大的前臼齿和近垂直牙齿中轴指向的原脊及下后脊),同时也具有比 *Eomys* 属进步的衍生性状(齿冠相对高,前边脊伸达舌侧并与原尖直接连接,下臼齿前边脊短,第一和第四谷长)。新属可能由 *Eomys* 演化而来,但起源何时、何地仍有待进一步的发现和研究。

小齿鼠属 *Leptodontomys* Shotwell, 1956

细小齿鼠(新种) *Leptodontomys pusillus* sp. nov.

种的特征 *Leptodontomys* 属中个体较小的一种;M1/2 舌侧前边脊弱;m1/2 的前边脊短,下中脊和下次脊发育弱;下臼齿的外谷和上臼齿的内谷宽。

一般说来,*Leptodontomys* 是一属个体很小、中新世时广布全北区的丘齿型始鼠。但 Engesser (1979)认为,北美"*Leptodontomys*"下门齿的腹侧没有纵沟而与欧洲的有所不同,因而他把欧洲原定为该属的始鼠更名为 *Eomyops*。我国尚未发现这一类始鼠的下门齿,所以暂时把它们都当作 *Leptodontomys* 属处理。

新种比欧洲的 *E. hebeiseni* 小很多,中脊发育也弱;个体虽与 *E. catalaunicus*、*E. bodvanus* 和 *E. oppligeri* 接近,但 M1/2 的舌侧前边脊没有那样显著,下臼齿的横脊发育弱,下中脊也短。与北美 *Leptodontomys* 的种相比,其个体稍小,M1/2 的舌侧前边脊亦弱,m1/2 的横脊略短,而第四内谷较发育。云南的小齿鼠比我国北方发现的 *L. gansus* 和 *L. lii* 都小,中脊相对短,但齿尖较齿脊显著。

小齿鼠(未定种) *Leptodontomys* sp.

材料中有采自雷老地点的上、下前臼齿各 1 枚。就牙齿的尺寸而言,既无法将其归入 *Leptodontomys pusillus*,也难以归入本文描述的其他属种。由于该始鼠的形态和大小更接近于小齿鼠属,这里当作该属的一个未定种处理。

始鼠科(属、种未定) Eomyidae gen. et sp. indet.

代表这一始鼠未定属、种的标本只有产自石灰坝和雷老的 3 枚下臼齿。其大小与 *Plesieomys mirabilis* 接近,但冠面上具有明显的、始鼠类动物中极不寻常的次生脊。此外,其下后尖和下内尖之间为一低脊连接,这一构造在 *Plesieomys mirabilis* 的下臼齿亦未见,

致使难以视其为后者的形态变异。

云南的发现表明，始鼠科在亚洲为广布型啮齿动物，不仅适应类似现代古北区的温带森林草原环境，同时也存活于与现代东洋区相似的热带、亚热带森林地区。禄丰和元谋古猿地点所发现的始鼠类动物，牙齿都为丘齿型，可能说明丘齿型始鼠比脊型始鼠更偏爱森林环境。

元谋雷老未发现有 *Leptodontomys pusillus*，只有该属的一个未定种。两个化石地点在始鼠组成上的细微差异，既可能是由于化石采样量的不足，也可能与两个动物群的时代不完全相同有关。但根据始鼠化石，目前还无法对两动物群的时代作出较精确的确定。

关键词：云南禄丰、元谋，中新世，石灰坝组、小河组，始鼠科

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EOMYIDS (MAMMALIA: RODENTIA) FROM THE LATE MIOCENE LUFENG AND YUANMOU HOMINOID LOCALITIES, YUNNAN

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Abstract　The material which forms the basis of this study was collected from two hominoid localities, Shihuiba of Lufeng and Leilao of Yuanmou, in Yunnan Province in the last twenty years. Five forms of eomyid rodents, *Plesieomys mirabilis* gen. et sp. nov., *Heteroeomys yunnanensis* gen. et sp. nov., *Leptodontomys pusillus* sp. nov., *Leptodontomys* sp. and Eomyidae gen. et sp. indet. are now recognized in the two late Miocene faunas. Morphologically, *Plesieomys* n. gen. shows some similarities to *Pseudadjidaumo* Lindsay, 1972 of North America, but the phylogenetic relationship of the new genus to the American genus is uncertain. *Heteroeomys* exhibits a mixture of primitive and advanced dental features of bunodont eomyids and might be descended from an early *Eomys* species. *Leptodontomys pusillus* is characterized by its smaller size, weaker developed lingual anteroloph on M1/2, narrow anterolophid and poor mesolophid and hypolophid on m1/2. The eomyid record in Yunnan indicates that eomyid rodents are a wide-ranging family in Asia, and that forested habitats are preferred more by eomyids with bunodont cheek-teeth than by eomyids with lophodont cheek-teeth.

Key words　Lufeng, Yuanmou, Yunnan, late Miocene, Shihuiba/Xiaohe Formation, Eomyidae

1　Introduction

Eomyidae are a group of fossil rodents with a wide distribution in the Holarctic Region during the Oligocene and Miocene time. The family, however, seems to be less important in the faunas of Asia than in Europe and North America. In China, knowledge of this family is based on a handful of specimens at a few localities. Up to now, only five genera, *Eomys*, *Eomyodon* and *Pseudotheridomys* from the middle and late Oligocene, and *Keramidomys* and *Leptodontomys* from the Miocene have been recognized in this country (Zheng and Li, 1982; Falhbusch et al., 1983; Wang and Emry, 1991; Qiu, 1994, 1996; Wang, 2002).

The materials described in this paper were collected from Shihuiba, Lufeng and Leilao, Yuanmou, hominoid localities in Yunnan Province, by screen washing in the years of 1983, 1999 and 2000. Both Shihuiba and Leilao are very productive sites containing abundant and diverse large and small mammals as well as hominoids (Qiu et al., 1985; Ni and Qiu, 2002). Based on small mammals, the age of the Shihuiba Fauna was assigned to the late Miocene (= Baodean Chinese Land Mammal Age), or an equivalence of younger MN11 or older MN12 of European Land Mammal Age) (Qiu and Storch, 1990; Qiu and Qiu, 1995; Qiu, 1995).

The study of rhizomyids, cricetids and murids from Yuanmou, however, suggests an older age for the Leilao Fauna than for the Shihuiba Fauna (Ni and Qiu, 2002; Storch and Ni, 2002). On the basis of rhizomyid biostratigraphy and Siwalik magnetostratigraphy, a date of about 9 Ma can be inferred for the Leilao Fauna, while the Shihuiba Fauna may be dated to as young as 8 Ma (Flynn et al., 1998; Ni and Qiu, 2002).

Although the eomyid materials from the two localities are limited, they are described here because they are new findings associated with hominoid remains, and are the only eomyid specimens from southern China.

2 Systematics

Eomyidae Depéret & Douxami, 1902
Plesieomys gen. nov.

Type species *Plesieomys mirabilis* sp. nov.

Etymology Plesi, Greek-near, a prefix; *Eomys* – a genus of Eomyidae with primitive bunodont type of cheek teeth; referring the affinities of the new genus with the ancient eomyid.

Diagnosis Relatively small-sized eomyids with bunodont cheek teeth, lingual and labial main cusps developed nearly equally, and weakly developed transverse loph(id)s. On M1 ~ 2 lingual anteroloph almost absent, mesoloph moderately long terminating usually as a minute terminal cuspule, metaloph poorly developed and lingual syncline generally symmetrical; On m1 ~ 2 hypolophid frequently absent or interrupted, anterolophid and posterolophid short and narrow, 1st and 4th synclines narrow.

Differential diagnosis *Plesieomys* differs from *Eomys* Schlosser, 1884 in having a cuspidate enlargement at the end of mesoloph on upper molars; longitudinal crest in the upper cheek teeth being situated more lingually, in the lowers more labially; and in more lingual extension of the 1st and 4th synclines in M1 and M2.

Plesieomys differs from *Eomyops* Engesser, 1979 and *Leptodontomys* Shotwell, 1956 in larger dimensions (except *E. hebeiseni*); having an enlarged end of the mesoloph on upper molars; and a much less distinct lingual anteroloph of M1 and M2.

Plesieomys differs from *Pentabuneomys* Engesser, 1990 in having smaller dimensions and lacking an enlargement of mesocone(id); weaker development of lingual anteroloph on M1 and M2; more reduced M3 and m3.

Plesieomys differs from *Pseudadjidaumo* Lindsay, 1972 in having an enlarged termination of the mesoloph and a weaker development of the lingual anteroloph on M1 and M2, and a weaker anterolophid and hypolophid on m1 and m2; more rapid changes of the anterolophid and posterolophid with wear in lower molars.

Plesieomys differs from *Ronquillomys* Jacobs, 1977 in smaller dimensions with more pronounced anterolophids on the lower molars; having a deeper 1st syncline on the M1 and M2, a broader 4th syncline on the lower molars; longitudinal crest situated more lingually in the upper cheek teeth, more labially in the lower cheek teeth; lower molars less narrow posteriorly than anteriorly.

Plesieomys differs from *Kansasimys* Wood, 1936 in smaller dimensions; having a deeper labial syncline in the upper cheek teeth and a deeper lingual syncline in the lower cheek teeth; hypolophid directed posteromedially from the entoconid rather than anteromedially.

Plesieomys mirabilis sp. nov.
(Fig. 1)

Eomyidae gen. et sp. nov. Qiu, 1994, fig. 2, p. 51 [part].

Eomyidae gen. et sp. indet. Ni and Qiu, 2002, table 1, p. 538 [part].

Derivatio nominis Mirabilis, Latin—fantastic, referring to frequent absence of hypolophid on m1 ~2, and the rapid changes in morphology with wear of the lower molars.

Holotype A left M1/2 (0.85 mm × 1.00 mm); V 14726.

Type locality Shihuiba, Lufeng County, Yunnan Province (China).

Statum typicum Layer 6, Shihuiba Formation, early Baodean, late Miocene.

Paratypes Lufeng: 12 isolated teeth (Layer 1 – 1 P4; L2 – 1 m1/2; L5 – 1 M1/2, 1 p4; L6 – 2 M1/2, 1 M3, 3 m1/2, 2 m3). V 14727.1 ~ 12.

Yuanmou: 11 isolated teeth (Loc. 9903 – 1 M1/2; Loc. 9904 – 1 M1/2, 2 m1/2; Loc. 9905 – 1 m1/2; Loc. 9906 – 1 M1/2, 1 p4, 3 m1/2, 1 m3). V 14728.1 ~ 11.

Measurements (see Table 1)

Table 1 Measurements of cheek teeth of *Plesieomys mirabilis* from Lufeng and Yuanmou (mm)

Tooth	N	Length		Width	
		Mean	Range	Mean	Range
P4	1	0.80		0.90	
M1/2	7	0.86	0.80 ~ 0.90	1.02	1.00 ~ 1.05
M3	1	0.65		0.85	
p4	2	0.88	0.85 ~ 0.90	0.78	0.75 ~ 0.80
m1/2	10	0.91	0.85 ~ 0.95	0.96	0.90 ~ 1.00
m3	3	0.88	0.85 ~ 0.90	0.88	0.85 ~ 0.90

Diagnosis Same as for genus.

Description The cheek teeth are bunodont with four nearly equally developed main cusps and relatively weak lophs. The longitudinal crest is situated lingual to the middle line of the tooth in the upper cheek teeth, and labial to the middle line in the lower cheek teeth.

The P4 is sub-quadrate in occlusal outline showing a short mesoloph and a poorly developed metaloph. The 2nd syncline extends lingually to the middle axis of the tooth.

The M1/2 is quadratic in outline and slightly wider than long. A lingual anteroloph is indistinct or absent. The protoloph is nearly perpendicular to the longitudinal axis, while the weakly developed metaloph is oriented more or less anteriorly. The longitudinal crest is curved, limited to a narrow, shallow and roughly symmetric lingual syncline. A moderately long mesoloph is directed slightly anteriorly in all 7 specimens, terminating as a minute cuspule in 6 teeth. All of the exterior synclines extend lingually to the middle line of the tooth, usually with the 2nd syncline the longest and the 1st syncline the narrowest.

The only M3 is small and rather worn; it has an elliptical occlusal outline with strong protocone and paracone, and an anteroloph and mesoloph weakly developed. The metacone is small and the hypocone is reduced in size.

The p4 is longer than wide, and narrower anteriorly than posteriorly. The protoconid is connected to the metaconid by a low crest. There is no distinct mesolophid. The longitudinal crest is strong and curved. The posterolophid is short, joining the posterior arm of the hypoconid. The hypolophid is absent or indistinct in one of the premolars.

The m1/2 is rectangular in occlusal outline and slightly longer than wide. The four main cusps are prominent, and the two internal cusps are higher than the two external cusps in unworn or slightly worn teeth. The thick metalophid is connected transversely to the protoconid, while the poorly developed hypolophid (absent or indistinct in 3 of the 8 specimens) is directed

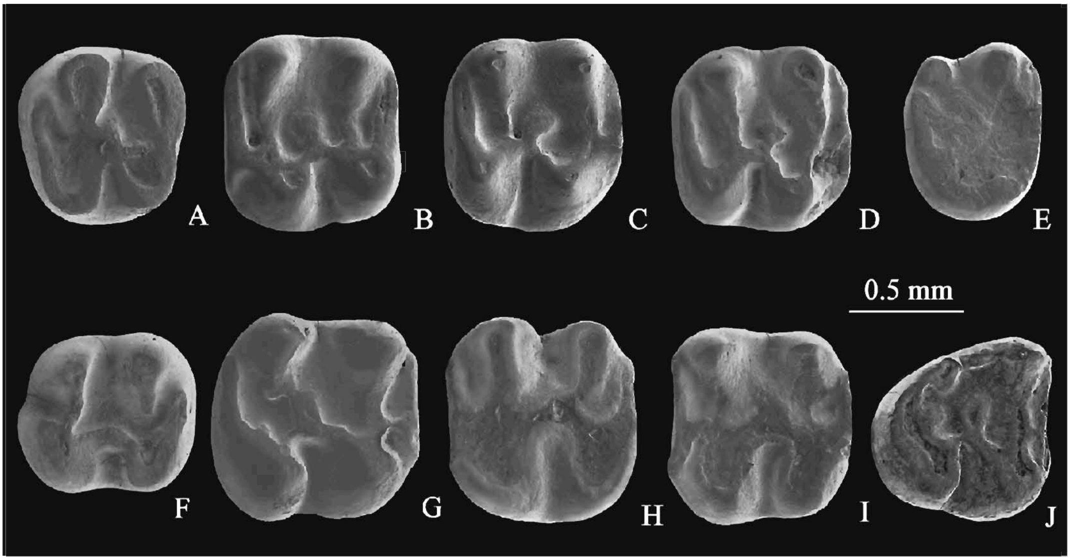


Fig. 1 *Plesieomys mirabilis* gen. et sp. nov. , cheek teeth, occlusal view
A. right P4 (V 14727.1); B. left M1/2, holotype (V 14726); C. right M1/2 (V 14728.2); D. right M1/2 (V 14728.6); E. right M3 (V 14727.7); F. left p4 (V 14727.4); G. right m1/2 (V 14728.3); H. left m1/2 (V 14728.4); I. left m1/2 (V 14728.8); J. right m3 (V 14727.11)

posteriorly to join the posterior arm of hypoconid. The longitudinal crest is curved and limited to a narrow labial syncline directed slightly posterointernally. The mesolophid is moderately long, joining the entoconid in three specimens that lack a hypolophid. The anterolophid joins the metalophid, it is moderately developed in unworn teeth, with wear it becomes shorter rapidly, remaining close to the metalophid. The posterolophid bends slightly to join the posterior arm of the hypoconid. In late stages of wear, the anterolophid and posterolophid become very thin, and the 1st and 4th synclines are very narrow.

The m3 is sub-triangular with a reduced entoconid. There is a distinct mesolophid with a minute cuspule at the distal end. A hypolophid is absent or interrupted.

Discussion This eomyid described above exhibits features of typical bunodont cheek teeth, which distinguish it from those genera with lophodont cheek-teeth, such as *Pseudotheridomys* and *Keramidomys* from Eurasia and *Paradjidaumo* from North America. It differs from some primitive species of *Rhodanomys* that show bunodont tooth patterns (Engesser, 1987, 1999), such as *R. transiens* and *R. hugueneyae* from the late Oligocene, in having a shorter mesoloph, a more complete longitudinal crest, a more deep 1st syncline on the upper molars, and a more pronounced 4th syncline on the lower molars.

The new genus shares some primitive characteristics with *Eomys*, the most representative eomyid with primitive bunodont cheek teeth, such as the four main cusps on cheek teeth, the longitudinal crest situated lingual to the middle of the tooth in upper cheek teeth and labial to the middle of the tooth in the lower cheek teeth, the protoloph and metaloph directed nearly perpendicular to the longitudinal axis, the greater depth of labial synclines in M1 and M2. This suggests that *Plesieomys* was closely allied to the Oligocene *Eomys* of Europe.

Morphologically, *Plesieomys* is very similar to *Pseudadjidaumo* Lindsay, 1972, especially in the size of cusps, the weak development of lophs, and in closure of the anterior and posterior valleys. However, it can not be assigned to *Pseudadjidaumo* because of the distinct differences, and the small sample size from Yunnan and the Mojave Desert of North America. Phylogenetic

relationship of *Pleieomys* to the North American genus *Pseudadjidaumo* is not clear.

It is likely that *Plesieomys mirabilis* descended from an early *Eomys*-like species. Nevertheless, where the new genus originated and where it further developed, are uncertain. Plausible candidates for the ancestry of the new eomyid are unknown, however, from both North America and Eurasia.

Heteroeomys gen. nov.

Type species *Heteroeomys yunnanensis* sp. nov.

Etymology Heter, Greek-different, a prefix; *Eomys*—a genus of Eomyidae; referring the affinities and differences of the new genus with the primitive eomyid.

Diagnosis Eomyids with bunodont cheek teeth, more or less unequally developed lingual and labial main cusps, and moderately long mesoloph(id). On M1 ~2 the lingual anteroloph is absent, but a long anteroloph that unites directly with the protocone; metaloph on upper molar, plus anterolophid and hypolophid on lower molars are weakly developed or interrupted.

Differential diagnosis *Heteroeomys* differs from *Eomys* Schlosser, 1884 in the absence of a lingual anteroloph on upper molar and weaker development of the anterolophid on the lower molars; longitudinal crest in the upper cheek teeth situated slightly lingual to the middle of the tooth, located labial to the middle of the tooth in the lower cheek teeth; synclines 1 and 4 very long and narrow in upper cheek teeth.

Heteroeomys differs from *Plesieomys* gen. nov. in larger size and slightly higher crowned teeth; unequally developed lingual and labial main cusps; longer anteroloph joining protocone directly on upper molar; better developed metaloph on M1/2, and hypolophid on m1/2.

Heteroeomys differs from *Eomyops* Engesser, 1979 and *Leptodontomys* Shotwell, 1956 in larger dimensions and higher crowned teeth (except *E. hebeiseni*); having longer anteroloph that lacks lingual part on upper molar; deeper 1st and 4th synclines in upper cheek teeth.

Heteroeomys differs from *Pentabuneomys* Engesser, 1990 in the absence of a lingual anteroloph on M1/2 and weaker development of the anterolophid on m1/2; having less rotund upper molars that lack well developed central cusps.

Heteroeomys differs from *Pseudadjidaumo* Lindsay, 1972 in having loph(id)s directed more perpendicular to the longitudinal axis; the absence of lingual anteroloph; and the anteroloph uniting directly with the protocone on upper molar.

Heteroeomys differs from *Ronquillomys* Jacobs, 1977 in having smaller dimensions with longer anterolophids on m1/2; having a deeper 1st syncline on M1/2, a broader 4th syncline on m1/2; longitudinal crest situated more lingually in M1/2, and more labially in m1/2.

Heteroeomys differs from *Kansasimys* Wood, 1936 in smaller dimensions; having deeper synclines; hypolophid directed posteromedially to join the posterolophid on lower molars.

Heteroeomys yunnanensis sp. nov.

(Fig. 2)

Eomyidae gen. et sp. nov. Qiu, 1994, fig. 2, p. 51 [part].
Eomyidae gen. et sp. indet. Ni and Qiu, 2002, table 1, p. 538 [part].

Derivatio nominis Named for the area of its discovery in Yunnan province of China.

Holotype A right M1/2 (1.00 mm × 1.15 mm); V 14729.

Type locality Shihuiba, Lufeng County, Yunnan Province (China).

Statum typicum Layer 5, Shihuiba Formation, early Baodean, late Miocene.

Paratypes Lufeng: 5 isolated teeth (Layer 1-1 m1/2; L6-1 DP4, 3 P4). V 14730.1 ~5.

Yuanmou: 6 isolated teeth (Loc. 9904-1 p4; Loc. 9906-2 P4, 1 dp4, 1 p4, 1 m1/2). V 14731.1 ~6.

Measurements (see Table 2)

Table 2 Measurements of cheek teeth of *Heteroeomys yunnanensis* from Lufeng and Yuanmou (mm)

Tooth	N	Length		Width	
		Mean	Range	Mean	Range
DP4	1	0.80		0.85	
P4	5	0.85	0.80~0.90	0.96	0.90~1.00
M1/2	1	1.00		1.15	
dp4	1	0.85		0.75	
p4	2	0.88	0.85~0.90	0.95	0.90~1.00
m1/2	2	1.03	1.00~1.05	1.00	0.95~1.05

Diagnosis Same as for genus.

Description The cheek teeth are bunodont and relatively higher crowned than in *Plesieomys*. The lingual main cusps are less prominent than the labial main cusps in the upper cheek teeth, and the lingual main cusps are stronger than the labial main cusps in the lower cheek teeth. The longitudinal crest is situated lingual to the middle line of the tooth in the upper cheek teeth, and labial to the middle line of the tooth in the lower cheek teeth.

The DP4 is trapezoid in occlusal outline due to the anteriorly protruding paracone. The P4 is subquadrate, and slightly wider than long. The longitudinal crest is short or interrupted, bearing a minute mesocone. The metaloph is connected to the anterior arm of the hypocone. There is no 1st syncline, and depth of the 2nd and the 4th synclines are subequal.

The M1/2 is quadratic in outline, slightly wider than long. The protoloph and metaloph are oriented nearly perpendicular to the longitudinal axis; they join the anterior arm of protocone and hypocone, respectively. The longitudinal crest is curved and limited to a narrow lingual syncline. The anteroloph extends to the anterolingal corner of the tooth then turns posteriorly to join the protocone, without any lingual part of the anteroloph. A moderately long mesoloph is directed anteriorly. The exterior synclines extend lingually to the middle of the tooth.

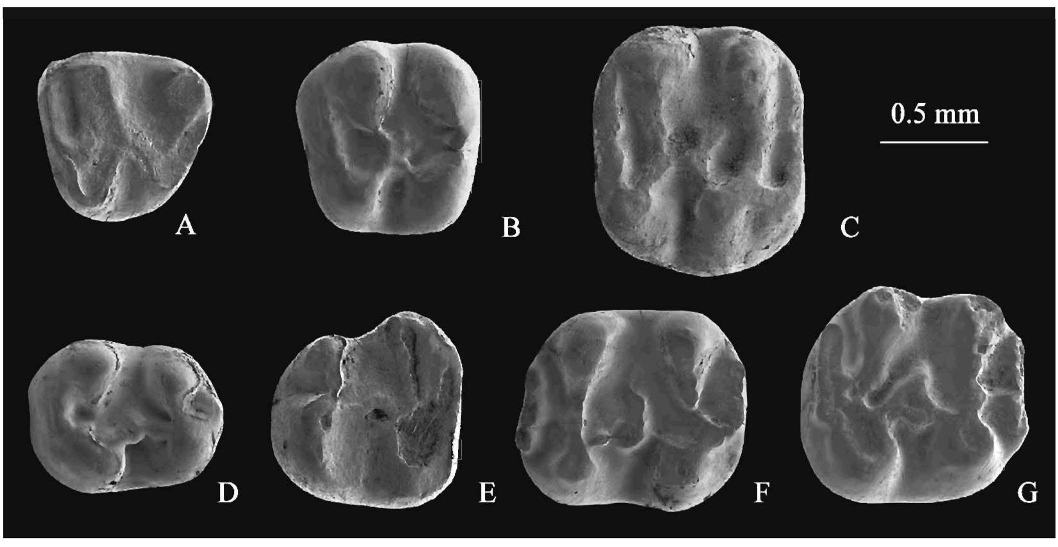


Fig. 2 *Heteroeomys yunnanensis* gen. et sp. nov., cheek teeth, occlusal view
A. right DP4 (V 14730.2); B. right P4 (V14730.3); C. right M1/2, holotype (V 14729); D. right dp4 (V 14731.4); E. left p4 (V 14731.5); F. left m1/2 (V 14730.1); G. right m1/2 (V 14731.6)

The dp4 is subrectangular in occlusal outline, longer than wide, and slightly narrower anteriorly. The protoconid is connected to the metaconid by a lower crest. There is a remnant of an anterolophid and a short mesolophid. The longitudinal crest is well developed and rather straight. The hypolophid is poorly developed, almost absent. The posterolophid is robust and connected the hypoconid to the entoconid. The p4 is similar to dp4, but larger in size and without any trace of an anterolophid.

The m1/2 is rectangular in occlusal outline and slightly longer than wide. The two main internal cusps are distinctly higher than the two main external ones. The metalophid is connected transversely to the protoconid, and the hypolophid is directed posteriorly to join the posterior arm of hypoconid. The thin longitudinal crest bears a minute mesoconid and constrains a relatively wide and short labial syncline. The mesolophid is moderately long and directed slightly anteriorly. The anterolophid is short and weak, connected to the middle of the metalophid. The posterolophid is robust and turns to join the posterior arm of the hypoconid.

Discussion Both the upper and lower teeth of this taxon are very homogeneous in shape, crown height and loph development. They are close in size and in morphology to the corresponding teeth of *Plesieomys mirabilis*, but their relatively higher crown height, unequally developed lingual and labial main cusps, and the long anteroloph of M1/2 exclude them from the morphological variation seen in other eomyid species. With the long and narrow anteroloph on M1/2 that extends far lingually to connect directly with the protocone, these specimens can not be referred to any known bunodont eomyid from Eurasia and North America. Thus, although the sample size is limited, it represents a new eomyid genus.

Compared with *Eomys*, the dentition of *Heteroeomys* exhibits a mixture of primitive and advanced features. It retains a number of primitive characters that show in the ancient bunodont eomyid genus, including the relatively large P4 and p4, orientation of the protoloph and metalophid more perpendicular to the longitudinal axis. More derived features are the relatively higher crown, the absence of a lingual anteroloph, the weak development of an anterolophid on the lower molars, the extended depth of the 1st and 4th synclines. It is likely that this genus is derived from an early *Eomys* species, but we do not know where or when it evolved.

Leptodontomys Shotwell, 1956

Leptodontomys pusillus sp. nov.

(Fig. 3A ~ F)

Leptodontomys sp. nov. 1 Qiu, 1994, fig. 2, p. 51.

Etymology Pusillus, Latin-tiny, referring to its small size.

Holotype A right M1/2 (0.70 × 0.80 mm); V 14732.

Type locality Shihuiba, Lufeng County, Yunnan Province (China).

Statum typicum Layer 6, Shihuiba Formation, early Baodean, late Miocene.

Paratypes Lufeng: 6 isolated teeth: L5-1 M1/2 (0.65 mm × 0.75 mm), 1 m1/2 (0.70 mm × 0.70 mm); L6-2 P4 (0.70 mm × 0.75 mm, 0.70 mm × 0.80 mm), 1 p4 (0.65 mm × 0.60 mm), 1 m1/2 (0.75 mm × 0.70 mm). V 14733.1 ~ 6.

Diagnosis Relatively small species of *Leptodontomys*, with poorly developed lingual anteroloph on M1/2, narrow anterolophid and weak mesolophid and hypolophid on m1/2, and wide labial syncline in lower cheek teeth and lingual syncline in upper cheek teeth.

Description The cheek teeth are characteristic of bunodont eomyids, with four well developed cusps. The longitudinal crest is situated lingual to the middle line of the tooth in the P4 and M1/2, and labial to the midline of the tooth in the p4 and m1/2. Depth of the 2nd and 4th synclines in the upper check teeth extend lingually past the middle line of the tooth, and the 4th synclines in the lower ones are also well developed.

The occlusal outline of the P4 is trapezoidal with a wider anterior portion than posterior portion and the labial side longer than the lingual side. A remnant of an anteroloph and a short mesoloph directed slightly anteriorly are seen in one of the two teeth. The longitudinal crest is short but distinct, and the posterior half is directed obliquely relative to the anterior half. The posteroloph joins the hypocone directly. The lingual syncline is moderately deep and wide.

The M1/2 are sub-quadrate in occlusal outline with wider lingual than labial side and slightly wider than long. The lingual part of the anteroloph is visible in the two teeth. The protoloph and metaloph are nearly perpendicular to the longitudinal axis. The longitudinal crest is strong and curved. The mesoloph is distinct, moderately long and directed toward the paracone. The lingual syncline is relatively wide and deep. Depth of the 2nd syncline extends lingually more then depth of the 3rd syncline.

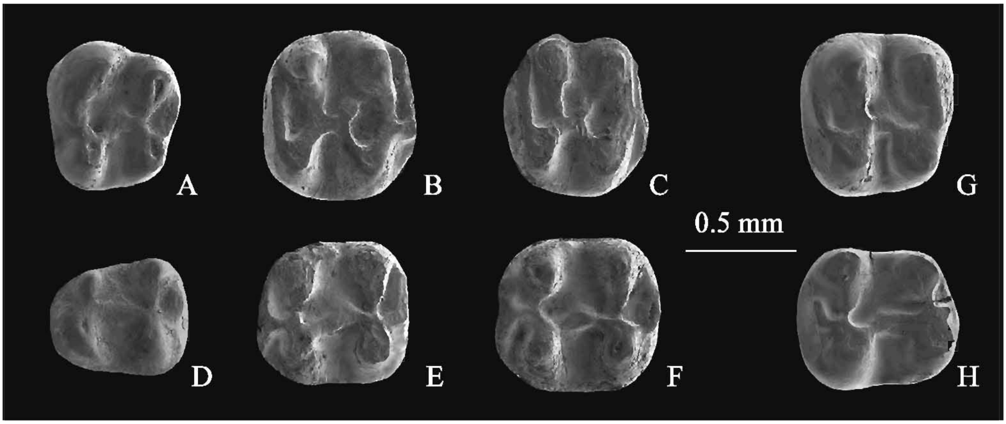


Fig. 3 *Leptodontomys pusillus* sp. nov. : A. left P4 (V 14733.4); B. right M1/2, holotype (V 14732); C. right M1/2 (V 14733.1); D. left p4 (V 14733.5); E. left m1/2 (V 14733.2); F. left m1/2 (V 14733.6); *Leptodontomys* sp. : G. right P4 (V 14734.1); H. right p4 (V 14734.2); cheek teeth, occlusal view

The p4 is longer than wide, and distinctly narrower anteriorly than posteriorly due to the relatively weakly developed metaconid. There is a low connection between the protoconid and metaconid. The longitudinal crest is low, but continuous. The posterolophid is reduced.

The m1/2 is sub-quadrate in occlusal outline. The anterolophid is well developed, but short transversely, connected with the metalophid by a thick crest. The prominent longitudinal crest is not straight; it is slightly curved posterior to the mesoconid. The labial syncline is very wide. The mesolophid is short or indistinct. The hypolophid is interrupted, free from or weakly joining the hypoconid. The posterolophid is prominent and joins the hypoconid nearly at a right angle to the posterolophid.

Comparison and discussion Since Engesser (1979) proposed the genus *Eomyops* based on material of the tiny bunodont eomyids from Europe, that had formerly been assigned to *Leptodontomys* (Hugueney and Mein, 1968; Fahlbusch, 1973; Fejfar, 1974), discussions on the generic membership of the European eomyids has been evolved (Fahlbusch et al., 1983; Qiu, 1994; Fahlbusch and Bolliger, 1996). Qiu (1994) noticed that *Leptodontomys gansus* Zheng & Li, 1982 from Songshan (Gansu) and Ertemte (Nei Mongol) is intermediate between European *Eomyops* and North American *Leptodontomys* described by Shotwell in most of the characters that Engesser emphasized to distinguish *Eomyops* from *Leptodontomys*. The presence of crenulated lower incisor seems to be an important diagnostic feature of *Eomyops* to distinguish from *Leptodontomys* (Engesser, 1979). It is not certain whether the lower incisor of the Chinese "*Lep-*

todontomys" is crenulated or not. Until its lower incisor is recovered, the nomen *Leptodontomys* for the small form of the Chinese bunodont eomyid is provisionally used.

Compared with most species of the European *Eomyops/Leptodontomys* group, *Leptodontomys pusillus* has a distinctly weaker development of the lingual anteroloph on upper cheek teeth, a narrower anterolophid and a weaker development of mesolophid and hypolophid on lower cheek teeth. In addition, it differs from *E. catalaunicus* (Hartenberger, 1966) in metaloph being nearly perpendicular to the longitudinal axis on M1/2, rather than anteriorly directed to join the longitudinal crest as in *E. catalaunicus*; it differs from *E. bodvanus* (Jánossy, 1972) in hypolophid being more perpendicular to the longitudinal axis. It differs from *Eomyops oppligeri* Engesser, 1990 in lack of a bifurcation of the mesoloph(id)s on M1/2 and m1/2. *Leptodontomys pusillus* is much smaller than *Eomyops hebeiseni* Kälin, 1997; it can be easily distinguished from the latter by its posterolophid joining hypoconid nearly at right angle on m1/2.

Leptodontomys pusillus is the smallest species of *Leptodontomys* known in China, and with distinctly narrower anteroloph(id) and weaker mesoloph(id). Additionally, it differs from *Leptodontomys gansus* Zheng & Li, 1982 in having weakly developed metalophid on m1/2, stronger posterolophid and wider labial syncline on m1/2; it differs from *Leptodontomys* sp. from Tunggur (Qiu, 1996) in having a wider labial syncline.

Leptodontomys pusillus differs from *Leptodontomys oregonensis* (Shotwell, 1956) from McKay Reservoir, Oregon, USA in having a poorly developed anterolophid and posterolophid, and the absence of a mesolophid on p4. It differs from *Leptodontomys* sp. from Black Butte, Oregon, USA in having smaller size, weaker development of lingual anteroloph and more extension of labial synclines on M1/2, as well as better developed 4th syncline, narrower anterolophid and poorly developed mesolophid on m1/2.

Leptodontomys sp.

(Fig. 3G, H)

A P4 (V 14734.1, 0.75 mm×0.85 mm) and a p4 (V 14734.2, 0.75 mm×0.70 mm) from Loc. 9905 of Yuanmou, are assigned to an indeterminate species of the genus *Leptodontomys*. The P4 is sub-quadrate in occlusal outline. A distinct mesoloph is absent or indistinct. The longitudinal crest is short, but strong. The metaloph is connected to the anterior arm of hypocone. There is no 1st syncline, depth of the 2nd and the 4th synclines are equally extended lingually to the middle of the tooth. The p4 is longer than wide, and narrower anteriorly than posteriorly. The protoconid is connected to the metaconid by a lower crest. There is a remnant of an anterolophid and a mesolophid. The longitudinal crest is strong and slightly curved. The posterolophid is short and joins the posterior arm of the hypoconid together with the hypolophid.

The two premolars resemble the corresponding teeth of *Leptodontomys pusillus* more closely in morphology and size than they do any other eomyid teeth from Yunnan, but they are slightly larger than those of the former. The available sample is too small to refer it to *L. pusillus*, or to definite a new species.

Eomyidae gen. et sp. indet.

(Fig. 4)

An m3 from Lufeng (V 14735, 0.90 mm×0.85 mm), and an m1/2 from Loc. 9905 (V 14736.1, 0.90 mm×0.90 mm) and two m1/2 from Loc. 9906 of Yuanmou (V 14736.2, 3; 1.00 mm×1.00 mm, 0.95 mm×0.95 mm) show secondary crests joining the mesolophid. They are close in size to specimens of *Plesieomys mirabilis*. There is a possibility that the morphology shown by the specimens represents intraspecific variation of *Plesieomys mirabilis*, but such secondary crests are unusual in other eomyids. In addition, a low connection between the metaconid and entoconid in the m1/2 and a distinct hypolophid in the m3 are not seen in the

present sample of *Plesieomys mirabilis*. Thus, it is inadvisable to refer these specimens to *Plesieomys mirabilis* or to create a new taxon for them without a larger sample.

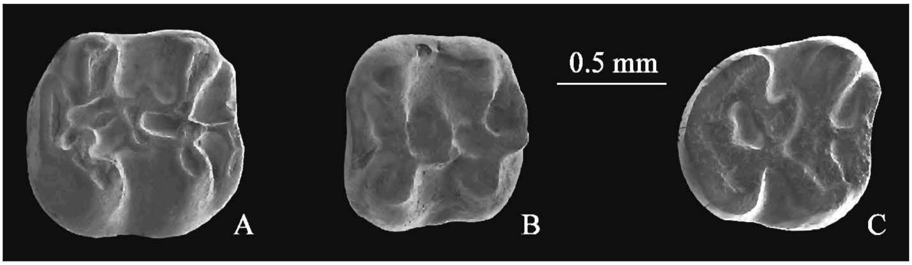


Fig. 4 Eomyidae gen. et sp. indet., cheek teeth, occlusal view
A. right m1/2 (V 14736.2); B. left m1/2 (V 14736.1); C. right m3 (V 14735)

3 Conclusions

The discovery of eomyids in Yunnan indicates that eomyid rodents are a wide-ranging family in Asia. They are not only adapted to a temperate open steppe environment similar to the recent Palaearctic Region, but also to a tropical or subtropical forest environment similar to the present Oriental Region. All the eomyids from Lufeng and Yuanmou have bunodont cheek-teeth. Thus it seems reasonable to infer that eomyids with bunodont cheek-teeth prefer forest habitats more than those with lophodont cheek-teeth. In addition, compared with other bunodont eomyids, all the eomyids from Yunnan share the same feature of weak development of transverse lophs. This is an assumed character of eomyids for preferring forested environments.

Eomyids recovered from the two hominoid localities include five forms, of which *Plesieomys mirabilis* is relatively common. Minor differences in composition between the two sites is probably due to sampling considering the inadequate amount of sediment processed, but a possibility of age difference for the two faunas can not be excluded. At the present, it is difficult to assess a more precise age for these faunas using the eomyids, because of the small sample size and limited knowledge of biochronology for these rodents. Among the Yunnan eomyids, only *Leptodontomys* is known outside this area, which appeared a little earlier in North America (late Oligocene) than in Europe (early Miocene), and survived until early Pleistocene in Europe.

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